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Cooperative web sharing against predators promotes group living in spider mites

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Abstract I examined spider mite cooperative web sharing against predation as a factor promoting group living. *Tetranychus urticae* and *Tetranychus kanzawai* infest leaf surfaces under webs made of silk threads. Experimental observation of predation by the predatory mite *Euseius sojaensis* on spider mites of different group sizes revealed that fewer spider mites were preyed upon when the web-building period before the attack was prolonged, suggesting that established webs help protect spider mites. Moreover, per capita predation on spider mites was diluted in larger groups. This was not due to predator satiation but seemingly because webs had been completed while the initial prey was consumed. Spider mites lived more closely together in the presence of a predator, showing that the degree of group living is facultative. In the presence of a preceding spider mite with an established web, a newcomer spider mite gain protection by taking residence in the established webs; sharing the web was not disadvantageous for the preceding mite. The proportion of individuals preyed upon did not differ between preceding and newcomer mites, suggesting that there was no interference against the latter. These interactions were consistent between heterospecific spider mites. Because there was no detectable

indirect interaction between mites sharing fresh webs, cooperative web sharing seemed to be a major force promoting group living in the spider mites. Moreover, the distances between spider mites did not differ between heterospecific and conspecific groups, demonstrating that mites living together do not distinguish between species; hence, heterospecific mites may cooperate and live together in the same manner as conspecifics.

Key words Apparent interspecific cooperation ▪ dilution effect ▪ group size ▪ indirect interaction ▪ cooperative web sharing

Introduction

Individuals living in a group can reduce their risk of predation by means of cooperative defense, the dilution effect, and by early warning (Krause and Ruxton 2002 and references therein). On the other hand, group members incur costs in terms of increased exposure to natural enemies and increased intraspecific competition (Fitzgerald 1993; Rasa 1997; Prokopy and Roitberg 2001). Therefore, the degree of conspecific aggregation should reflect the costs and benefits of group living (Rasa 1997; Spieler 2003; Semeniuk and Dill 2004; Despland and Huu 2007). From this viewpoint, heterospecific individuals may also live together in a group when the benefit of interspecific grouping to individuals overwhelms the cost of interspecific competition between them. These interspecific interactions have been reported among conspecific organisms such as birds (Krams and Krama 2002), spiders (Hodge and Storfer-Issera 1997), shellfishes (Briones-Fourzan et al. 2008), and mammals (Barry and Mundy 2002). This study reports that related spider mite species with common potential predators live together and cooperate in the same manner as conspecifics; this co-habitation is probably a byproduct of intraspecific

52 cooperation.

53 *Tetranychus urticae* and *Tetranychus kanzawai* are polyphagous spider mites
54 (e.g., Jeppson et al. 1975; Gotoh et al. 1999). They live together on dozens of wild
55 and cultivated host plant species and often co-occur on the same plant specimen
56 (Kondo and Takafuji 1985; Morishita 1992; 1997; Takafuji and Morishita 2001;
57 Osakabe et al. 2002; Ohno et al. 2010). Mated mite adult females (founder
58 individuals) construct complicated, irregular webs on leaf surfaces (Saito 1983),
59 feeding and reproducing inside the webs, and ultimately forming aggregations that
60 include juveniles that also contribute to the web building (Hazan, 1974; Clotuche et
61 al., 2009). Mated adult females of these mites disperse to new hosts, primarily by
62 walking (Kondo and Takafuji 1985; Margolies and Kennedy 1985; Morishita 1992;
63 1997). Ambulatory dispersing adult females of *T. urticae* often follow trails left by
64 preceding females and join webs built by conspecifics, which results in group living
65 at a new colony site (Yano 2008). Although mites normally aggregate on their host
66 plants (Strong et al. 1997; Oku et al. 2005; Yano 2008), a typical tetranychid colony
67 in the wild contains less than five adult females (Yano, unpublished data).

As an ultimate factor promoting conspecific group living of spider mites, cooperative defense against predators using webs has been reported in the bamboo spider mite *Stigmaeopsis longus* (Saito 1986a; 1986b; Mori et al. 1999). In contrast, virtually no attention has been paid to the benefit of group living as cooperative defense in either *T. urticae* and *T. kanzawai*. This may be because spider mites of this genus never exhibit aggressive defensive behaviors, though aggressive defense against predators does occur in mites belonging to the genus *Stigmaeopsis* and in social caterpillars (McClure and Despland 2011). Another reason for the lack of attention to the benefit of cooperative defense in *Tetranychus* may be that specialist predatory mites such as *Phytoseiulus persimilis* and *Neoseiulus womersleyi* can easily suppress spider mite populations at high densities (e.g., Chant 1961; Hamamura 1986), which implies that collective webs are ineffective as a defense. However, the apparently antagonistic interactions between spider mites and specialist predatory mites may only be one potential outcome because spider mite webs should exclude remaining potential predators. Indeed, some studies have suggested that spider mite webs are effective against generalist predators (McMurtry

et al. 1970; Sabelis and Bakker 1992). Therefore, interactions between spider mites and generalist predatory mites should be examined as a factor promoting spider mite group living.

In general, the effectiveness of a defensive trait against potential enemies becomes apparent only when the trait is absent. For example, some myrmecophytes are only heavily attacked by herbivorous insects when symbiont ants, i.e., the defensive trait of the plant, are artificially excluded from the plants (Vasconcelos 1991; Gaume et al. 1997). From this viewpoint, antagonistic interactions between spider mites and potential predators will be detectable only before founder spider mite females (that had dispersed from previous host plants) complete webs on new host plants. *Euseius sojaensis* is a generalist predatory mite that feeds on plant products and many spider mite species (Osakabe et al. 1986; Amano 1996). Although *E. sojaensis* cannot penetrate completed spider mite webs (Osakabe 1988; Ozawa and Yano 2009), the predatory mite readily preys on spider mites outside the webs (Ozawa and Yano 2009). Therefore, the predator is considered to be a typical potential predator of *T. urticae* and *T. kanzawai*.

In this study, I examine why the spider mite species *T. urticae* and *T. kanzawai* live in groups, and why different spider mite species may live close together, by investigating cooperative web sharing against the potential predator *E. sojaensis*.

Materials and methods

Mites

Single populations of the two spider mite species were collected in Kyoto, Japan; that of *T. urticae* (green form) was collected from a rose garden, and the *T. kanzawai* population was collected from a strawberry garden. Both populations were maintained on expanded primary leaves of the kidney bean *Phaseolus vulgaris* (Leguminosae), pressed onto water-saturated cotton in Petri dishes (90-mm diameter, 14-mm depth). The *E. sojaensis* study population was collected from kudzu vines *Pueraria lobata* (Willd) Ohwi (Leguminosae) in Kyoto and was reared on tea pollen on 50 × 50-mm squares of Parafilm (Parafilm M; American National Can Co.,

116 Chicago, IL, USA) placed on water-saturated cotton in Petri dishes (for details, see
117 Shirotsuka and Yano 2011). The dishes were placed in transparent plastic containers
118 and kept at 25 ± 2°C and 50 ± 5% relative humidity, with a photoperiod of 16L8D
119 (hereafter described as “laboratory conditions”).

120 Adult females of the spider and predatory mites used in the following
121 experiments were similar in size (≤0.5 mm). Detailed observations and transfer using
122 a fine brush were possible only under a stereomicroscope. Webs are usually invisible
123 even under a microscope (e.g., Clotuche et al. 2009). Because mated adult females
124 represent the dispersing stage of spider mites, I used 2- to 4-day-old mated females
125 (hereafter “females”) of *T. urticae* and *T. kanzawai* in the following experiments. By
126 using these females as prey, I simulated an early stage of web building in the
127 presence or absence of predators.

128

129 Effects of group size and webs on predation rates on spider mites

130

131 To examine effects of spider mite group size and the degree of web building on

132 predation by *E. sojaensis*, I confined different numbers (1, 2, and 4) of each spider
133 mite species on 15 × 15-mm bean leaf squares. Unless otherwise noted, I thereafter
134 used bean leaf squares of the same size. One to four adult females correspond to a
135 typical colony size of tetranychid mites in the wild (Yano, unpublished data). I then
136 introduced an *E. sojaensis* female onto each leaf square after different time lags (0, 1,
137 4, and 24 h), which allowed spider mites to build different degrees of webs before
138 predator attack. I did not monitor at more frequent intervals because spider mites
139 seem to have diurnal rhythms (e.g., Clotuche et al. 2011). I used 3- to 5-day-old
140 starved *E. sojaensis* females that had previously been isolated for 48 h in 1.5-ml
141 microtubes (Treff AG, Degersheim, Switzerland) with a water droplet. This was to
142 promote immediate predation and to easily judge predation, because the transparent
143 body of a starved predator turns a vivid vermillion after consuming prey. Thereafter,
144 all starved *E. sojaensis* were prepared in the same manner. No *E. sojaensis* females
145 died during the starvation treatment. The number of replicates for each combination
146 of group sizes and time lags was >20. Preliminary experiments showed that
147 predation by a starved *E. sojaensis* female on a *T. urticae* or a *T. kanzawai* female on

148 a leaf square reached a plateau 12 h after introduction (Fig. 1). Therefore, the
149 proportion of consumed prey (predation rates) in all experiments was measured 24 h
150 after predator introduction. The data were analyzed with a Wald test (SAS Institute
151 Inc. 1998).

152 To examine whether satiation of the predators may have limited predation rates
153 of the above experiment, potential consumption by *E. sojaensis* was measured. To
154 prepare living prey females that do not walk or produce webs, I used adult females
155 of *T. urticae* and *T. kanzawai* that had been subjected to a sub-lethal intensity of
156 ultraviolet irradiation (253.7-nm wavelength, 0.45 W m^{-2} for 1 h) using a GL-6
157 sterilization lamp (6 W; Ultra-Violet Box, Sogorikagaku Glass Works Co., Kyoto,
158 Japan). I supplied four prey females to each starved predatory mite on a leaf square.
159 After 24 h, the number of consumed prey was recorded.

160 To examine whether spider mite eggs deposited during the experimental period
161 may have affected predation rates in the experiment, egg consumption by *E.*
162 *sojaensis* in the same period was examined. I confined a female of each spider mite
163 species on the bean leaf squares. After 24 h, I carefully removed the females with

minimal damage to the webs, and counted the number of eggs laid. All spider mite eggs were deposited within webs. I then introduced a starved *E. sojaensis* onto each leaf square. After another 24 h, I counted the number of consumed eggs.

Degree of spider mite group living in response to a predator

To examine whether spider mites lived together in response to predators, I measured the distance between pairs of spider mite females in relation to predator presence. I introduced two females onto each of 24 leaf squares for each spider mite species. To avoid predation during observation, I allowed the females to build webs for 24 h under laboratory conditions, after which the females were sufficiently protected by webs (see “Results”). I then introduced one starved *E. sojaensis* female each onto half of the leaf squares (n = 12, predator presence) for each spider mite species while the rest of the squares served as controls (n = 12, predator absence for each species). Because the body length of *E. sojaensis* was <0.5 mm, leaf area occupied by the predator was <1/1,000 of the leaf square, which may be considered negligible. After

1, 4, and 24 h, I measured the distances between the centers of the idiosomas of the female spider mites to the nearest 1 mm as a degree of group living. As decimal fractions were rounded off, the minimum distance was 1 mm. A replicate (*T. urticae*, predator absence) in which a spider mite female escaped from the leaf square was excluded from the data. A three-way ANOVA (SAS Institute Inc. 1998) was then performed on square root-transformed data.

Pros and cons of lodging and hosting spider mites in the presence of a predator

To simulate the conditions in which a preceding spider mite female has already established a web, an initial female (hosting female) was introduced to a leaf square. After 24 h, when the whole surface of the leaf square was more or less covered by web, a second lodging female and a starved *E. sojaensis* female were introduced to the square. To discriminate between conspecific spider mites, I randomly selected one and marked it with a dab of blue pigment ink on the dorsal setae. I examined four combinations (i.e., *TuTu, TkTk, TuTk* and *TkTu*) of the two spider mite species.

196 The number of replicates for each combination was >20. Predation rates were
197 measured 24 h after predator introduction.

198 To examine costs and benefits of hosting and lodging, predation rates on
199 hosting and lodging females were compared with those in the absence of respective
200 partners. Thus, the predation rate on lodging females was compared with that of
201 solitary females without webs (group size = 1, time lag = 0 h in the above
202 experiment) while that on hosting females was compared with that on solitary
203 females with webs (group size = 1, time lag = 24 h). The rates were compared using
204 Fisher's exact probability test.

205

206 Indirect interaction between spider mites sharing webs in the absence of a predator

207

208 Indirect interactions among herbivores include both exploitative competition and
209 plant-mediated interactions (e.g., Kaplan and Denno 2007). To examine whether
210 there were either competitive or facilitative indirect interactions between spider mite
211 females sharing webs, I introduced one female (initial female) onto each of forty 10

212 × 10-mm leaf squares per species (*T. urticae* and *T. kanzawai*); 40 squares served as
213 controls without initial females. These leaf squares were maintained under
214 laboratory conditions. After 24 h, I carefully removed the initial females with
215 minimal damage to the webs, and counted the number of eggs laid. I then introduced
216 one *T. urticae* female (test female) each onto half of the leaf squares in each
217 treatment and one *T. kanzawai* female (test female) onto each of the remaining
218 squares. After another 24 h, I counted the cumulative egg numbers laid and
219 calculated egg numbers laid by each test female by subtracting the egg number of the
220 initial female from the cumulative number. Because the number of eggs laid within a
221 certain period is considered the most sensitive performance index of spider mite
222 females (Yano et al. 1998; Gotoh et al. 1999; Agrawal 2000; Yano et al. 2003), any
223 indirect interaction, either exploitative competition or plant mediated interaction,
224 between females sharing webs should result in lower (or higher) egg numbers laid by
225 the test female. A one-way ANOVA (SAS Institute Inc. 1998) was performed on the
226 data for each test female species.
227

228 Do spider mites living together distinguish between species?

229

230 To examine whether females living together distinguish between species, I
231 introduced two females onto a 15 × 15-mm leaf square in the following
232 combinations: two *T. urticae* (n = 32), two *T. kanzawai* (n = 31), or one female of
233 each species (n = 33). I then measured the distances between females to the nearest 1
234 mm at 3, 6, 12, 24, and 48 h after the introduction. A one-way ANOVA (SAS
235 Institute Inc. 1998) was performed on square root-transformed data for each time
236 point.

237

238 **Results**

239

240 Effects of group size and webs on predation rates on spider mites

241

242 Both group size and time lag for web building had significant effects on per
243 capita predation rates on *T. urticae* and *T. kanzawai* (Table 1). Decreased predation

with increased time lag indicates that completed webs may effectively defend spider mites from predation while decreased (per capita) predation with increasing group size indicates a dilution effect (Fig. 2). Each *E. sojaensis* individual consumed less than one spider mite in average.

The number (± SE) of immobilized spider mites consumed by *E. sojaensis* individuals in 24 h was 2.24 ± 0.17 (n = 21) for *T. urticae* and 3.30 ± 0.16 (n = 20) for *T. kanzawai*. These results demonstrate that predators consuming at most one living spider mite in a 24-h period in this experiment were not satiated. Predators may have consumed less active spider mites rather than those that were immobilized because of the protection provided by webs and the mobility of prey mites (possible avoidance behavior).

In addition, the number (± SE) of spider mite eggs consumed by *E. sojaensis* individuals in 24 h was 0.43 ± 0.23 (n = 14) for *T. urticae* and 1.08 ± 0.46 (n = 13) for *T. kanzawai*, while initial egg numbers were 7.21 ± 0.49 (n=14) and 9.00 ± 0.60 (n=13), respectively.

260 Degree of spider mite group living in response to a predator

261

262 The distances between females differed significantly with respect to the presence of
263 a predator (Table 2), although the differences became less obvious over time after
264 predator introduction (Fig. 3). Thus, spider mite females lived more closely together
265 in response to predator presence. In addition, no spider mites were preyed upon
266 during this experiment.

267

268 Pros and cons of lodging and hosting spider mites in the presence of a predator

269

270 The predation rates on lodging and hosting females did not differ significantly (Table
271 3, comparison A), suggesting that there was no interference against lodging females.
272 Indeed, interference behaviors among females were never observed. Moreover, the
273 predation rate on lodging females was lower than that on solitary mites without webs
274 (Table 3, comparison B); the predation rate on hosting females did not differ from
275 that on solitary females with webs (Table 3, comparison C). These patterns were

276 consistent across all combinations of spider mite species.

277

278 Indirect interaction between spider mites sharing webs in the absence of a predator

279

280 The number of eggs laid by a test female within 24 h did not differ among treatments
281 for either *T. urticae* (Fig. 4a), *T. kanzawai* (Fig. 4b), indicating that there was
282 virtually no indirect interaction between heterospecific and conspecific mites sharing
283 fresh webs.

284

285 Do spider mites living together distinguish between species?

286

287 Up to 24 h after introduction, the average distance between spider mite females was
288 approximately 3 mm (on a 15 × 15-mm square) for all combinations. That is, the
289 mites lived relatively close together even in the absence of a predator. The distance
290 between females did not differ significantly among heterospecific and conspecific
291 groups at any point; P = 0.18 (3 h), 0.84 (6 h), 0.42 (12 h), 0.49 (24 h), and 0.25 (48

292 h) (Fig. 5). These data show that spider mite females living together do not
293 distinguish between species.
294
295 **Discussion**
296
297 The decrease in predation on spider mites with increased time lag for web building
298 indicates that established webs protected spider mites from predation. Previous
299 studies (McMurtry et al. 1970; Osakabe 1988; Sabelis and Bakker 1992; Ozawa and
300 Yano 2009) also report that established spider mite webs are effective against
301 generalist predators. Although spider mite webs contain many eggs, all eggs are
302 deposited within webs where *E. sojaensis* cannot easily access. Therefore, *E.*
303 *sojaensis* consumed only a small fraction of the eggs. Moreover, considering the
304 relative size of a spider mite (0.5 mm) and an egg (<0.15mm; Crooker 1985), effects
305 of egg consumption on predation rates seemed negligible, if any. Compared with the
306 spider mite short generation time of about 10 days at 25ºC, a web establishment
307 period as long as 24 h may be considerable. Therefore, any trait that reduces

308 predation risk during this 24-h period should confer selective advantage to the spider
309 mites. From this viewpoint, group living during web production seems to reduce the
310 predation rate on spider mites. This dilution effect was not due to the satiation of
311 predatory mites because they had the potential to consume more than twice the
312 number of immobilized prey in the same period. Therefore, it is likely that the tested
313 predatory mites were unable to consume more living prey because webs had been
314 completed beforehand.

315 The closer group living of spider mites in the presence of a predator implies
316 that the degrees of group living in the two spider mite species are facultative; i.e., the
317 benefit of closer group living in the presence of a predator may outweigh its possible
318 cost. Because no spider mite was preyed upon in the presence of previously
319 established webs, indirect cues for predator presence, e.g., odors from injured
320 conspecifics (Grostal and Dicke 1999; Oku et al. 2003), may be ruled out; the spider
321 mites living closely together may have instead detected direct cues for predator
322 presence, e.g., odors and wastes (Grostal and Dicke 1999, 2000; Pallini et al. 1999).
323 The closer group living of spider mites in the presence of a predator had decreased

over time probably because amount of established webs may have affected spider mites' behaviors and/or because they became increasingly aware that predators were unable to access them.

Dispersing adult females of *T. urticae* readily follow conspecific trails and join conspecific webs (Yano 2008). The benefit of these behaviors was explicitly demonstrated in the present study in the practice of cooperative web sharing. In the presence of a predator and a preceding spider mite with an established web, a secondarily introduced (lodging) female gained protection from predation by lodging in the web: sharing the web was not a disadvantage for the hosting female. This asymmetric cost-benefit of lodging and hosting females seems to explain why they shared webs. Otherwise, if the benefit of a lodging individual were achieved at a cost for the hosting individual, such altruistic behavior should have evolved only between conspecific relatives. Moreover, the proportion of predated individuals did not differ between hosting and lodging mites, suggesting that there was no interference against the latter. The above interactions were consistent in pairs of heterospecifics, indicating that spider mites sharing webs do not distinguish between species.

340 Although there was no direct interference between spider mites sharing webs,
341 living in proximity to others may have fitness costs associated with indirect
342 competition, i.e., exploitive and/or plant-mediated competition (Tilman 1982;
343 Kaplan and Denno 2007). However, such indirect competition seemed negligible
344 both within and between spider mite species sharing webs. Because the feeding
345 modes of the two related spider mite species were identical, fine-scale resource
346 partitioning between individuals living in close proximity (e.g., Daugherty 2009)
347 seems unlikely. Oku et al. (2009) demonstrated a web-building cost for *T. urticae*
348 adult females in terms of reduced egg production during the initial 24 h of web
349 building. Therefore, females introduced secondarily may have offset the costs of
350 possible indirect competition with initial females by reducing web-building costs,
351 that is, by sharing established webs. There may be some competition after web
352 establishment, i.e., following the initial 24 h of web building; however, living in
353 proximity to others after the initial 24 h would no longer be necessary because spider
354 mites were seldom preyed upon after that time. The rarity of predation after this 24 h
355 period is attributable to (1) spider mites remaining within webs and (2) continued

356 feeding within webs that are extended over leaf surfaces, leading to heavy infestation
357 (Yano, unpublished data). Web extension in this manner is reflected in Figure 5,
358 which shows that between-female distances increased slightly after 24 h of web
359 building. Therefore, living in proximity to others during web establishment should
360 always be advantageous in the end, perhaps explaining why the spider mites always
361 live in groups. Le Goff et al. (2010) reported significant positive group effects on
362 egg production in *T. urticae* virgin females. However, such a positive group effect on
363 egg production was not detected in the present experiment using mated females (i.e.,
364 dispersing stage) of the two spider mite species.

365 Although the two spider mite species co-occur on the same host plants (Kondo
366 and Takafuji 1985; Morishita 1992; 1997; Takafuji and Morishita 2001; Osakabe et
367 al. 2002; Ohno et al. 2010) and have the potential to live closely together on a single
368 leaf, as demonstrated here, strong natural selection for heterospecific cooperation (in
369 comparison to conspecific cooperation) remains questionable. The apparent
370 cooperation between heterospecifics may rather be a byproduct of cooperation
371 between conspecifics that live together. The two spider mite species discriminate to

some extent between heterospecific and conspecific mates before copulation (Ozawa and Takafuji 1987), suggesting that there has been selection for discrimination between species when necessary. Therefore, the fact that the spider mites did not distinguish between species when living together on a leaf likely indicates that some advantage is gained by sharing webs with heterospecifics.

There is a complete post-mating reproductive barrier between *T. urticae* and *T. kanzawai* (Ozawa and Takafuji 1987), indicating that they are distinct biological species. Therefore, the apparent cooperative web sharing between these two species raises the question of how the two distinct species evolved. The most plausible explanation may be allopatric speciation; *T. urticae* expanded its distribution to southwestern areas of Japan (Kyoto) as recently as the late 1970s (Gotoh and Shinkaji 1981).

Although spider mite webs afford effective protection against generalist predatory mites, the webs are ineffective against mites that specialize in preying on web-spinning spider mites (McMurtry et al. 1970; Sabelis and Bakker 1992). This is an example of apparent trade-offs in adaptation to different prey (Levins and

388 MacArthur 1969). Moreover, some specialist predatory mites use spider mite webs
389 as prey-searching cues (Pratt and Croft 1999; Roda et al. 2001; Furuichi et al. 2005).
390 Therefore, group living of spider mites may be costly against such specialist
391 predatory mites. This possible trade-off in cooperative web sharing against specialist
392 and generalist predatory mites may in turn determine spider mite optimal group sizes
393 in the wild; this is a topic that remains to be addressed in future investigations.
394
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400
401 **References**
402 Agrawal AA (2000) Host range evolution: adaptation and trade-offs in fitness of
403 mites on alternate hosts. Ecology 81:500-508

404 Amano H (1996) Natural enemies. In: Ehara S, Shinkaji N (eds) Principles of Plant
405 Acarology. Zenkoku Noson Kyoiku Kyokai, Tokyo, pp 159-174 (in Japanese)
406 Barry RE, Mundy PJ (2002) Seasonal variation in the degree of heterospecific
407 association of two syntopic hyraxes (*Heterohyrax brucei* and *Procavia capensis*)
408 exhibiting synchronous parturition. Behav Ecol Sociobiol 52:177-181
409 Briones-Fourzán P, Ramírez-Zaldívar E, Lozano-Álvarez E (2008) Influence of
410 conspecific and heterospecific aggregation cues and alarm odors on shelter
411 choice by syntopic spiny lobsters Biol Bull 215:182-190
412 Chant DA (1961) An experiment in biological control of *Tetranychus telarius* (L.)
413 (Acarina: Tetranychidae) in a greenhouse, using *Phytoseiulus persimilis*
414 Athias-Henriot (Phytoseiidae). Can Entomol 93:437-443
415 Clotuche G, Le Goff G, Mailleux AC, Deneubourg JL, Detrain C, Hance T (2009)
416 How to visualize the spider mite silk? Microsc Res Techniq 72:659-664
417 Clotuche G, Mailleux AC, Astudillo FA, Deneubourg JL, Detrain C (2011) The
418 formation of collective silk balls in the spider mite *Tetranychus urticae* Koch.
419 PLos ONE 6(4): e18854

420 Crooker A (1985) Embryonic and juvenile development In: Helle W, Sabelis MW
421 (eds) Spider Mites: their Bilology, Natural Enemies and Control. Vol. 1A
422 Elsevier, Amsterdam, pp 149-163
423 Daugherty MP (2009) Specialized feeding modes promote coexistence of competing
424 herbivores: insights from a metabolic pool model. Environ Entomol 38:667-676
425 Despland E, Huu AL (2007) Pros and cons of group living in the forest tent
426 caterpillar: separating the roles of silk and of grouping. Entomol Exp Appl
427 122:181-189
428 Fitzgerald TD (1993) Sociality in caterpillars. In: Stamp NE, Casey TM (eds)
429 Caterpillars: ecological and evolutionary constraints on foraging. Chapman &
430 Hall, New York, pp 372-403
431 Furuichi H, Yano S, Takafuji A, Osakabe Mh (2005) Prey preference of the predatory
432 mite *Neoseiulus womersleyi* Schicha is determined by spider mite webs. J Appl
433 Entomol 129:336-339
434 Gaume L, Mckey D, Anstett MC (1997) Benefits conferred by “timid” ants: active
435 anti-herbivore protection of the rainforest tree *Leonardoxa africana* by the

436 minute ant *Petalomyrmex phylax*. Oecologia 112:209-216

437 Gotoh T, Shinkaji N (1981) Critical photoperiod and geographical variation of
438 diapause induction in the two-spotted spider mite, *Tetranychus urticae* Koch
439 (Acarina: Tetranychidae). Jap J Appl Entomol Zool 25:113-118 (in Japanese,
440 with English summary)

441 Gotoh T, Gomi K, Nagata T (1999) Incompatibility and host plant differences among
442 populations of *Tetranychus kanzawai* Kishida (Acari: Tetranychidae). Appl
443 Entomol Zool 34:551-561

444 Grostal P, Dicke M (1999) Direct and indirect cues of predation risk influence
445 behavior and reproduction of prey: a case for acarine interactions. Behav Ecol
446 10:422-427

447 Grostal P, Dicke M (2000) Recognising one's enemies: a functional approach to risk
448 assessment by prey. Behav Ecol Sociobiol 47:258-264

449 Hamamura T (1986) Studies on the biological control of Kanzawa spider mite,
450 *Tetranychus kanzawai* Kishida by the chemical resistant predacious mite,
451 *Amblyseius longispinosus* (Evans) in tea fields (Acarina: Tetranychidae,

452 Phytoseiidae). Bull Natl Res Inst Tea 21:121-201 (in Japanese with English
453 summary)
454 Hazan A, Gerson U Tahori AS (1974). Spider mite webbing. I. The production of
455 webbing under various environmental conditions. Acarologia 16:68-84
456 Hodge MA, Storfer-Issera A (1997) Conspecific and heterospecific attraction: a
457 mechanism of web-site selection leading to aggregation formation by
458 web-building spiders. Ethology 103:815-826
459 Jeppson LR, Keifer HH, Baker EW (1975) Mites Injurious to Economic Plants.
460 University of California Press, Berkeley
461 Kaplan I, Denno RF (2007) Interspecific interactions in phytophagous insects
462 revisited: a quantitative assessment of competition theory. Ecol Lett 10:977-994
463 Kondo A, Takafuji A (1985) Resource utilization pattern of two species of
464 tetranychid mites (Acari: Tetranychidae). Res Popul Ecol 27:145-157
465 Krams I, Krama T (2002) Interspecific reciprocity explains mobbing behaviour of
466 the breeding chaffinches, *Fringilla coelebs*. Proc R Soc Lond B 269: 2345-2350
467 Krause J, Ruxton GD (2002) Living in groups. Oxford University Press, Oxford

468 Le Goff GJ, Mailleux A-C, Detrain C, Deneubourg J-L, Clotuche G, Hance T (2010)
469 Group effect on fertility, survival and silk production in the web spinner
470 *Tetranychus urticae* (Acari: Tetranychidae) during colony foundation. Behaviour
471 147:1169-1184
472 Levins DA, MacArthur RH (1969) A hypothesis to explain the incidence of
473 monophagy. Ecology 50:910-911
474 Margolies DC, Kennedy GG (1985) Movement of the two-spotted spider mite
475 *Tetranychus urticae* Koch (Acari: Tetranychidae), among hosts in a
476 corn-peanut agroecosystem. Entomol Exp Appl 37:55-61
477 McClure M, Despland E (2011) Defensive responses by a social caterpillars are
478 tailored to different predators and change with larval instar and group size.
479 Naturwissenschaften 98:425-434
480 McMurtry JA, Huffaker CB, van de Vrie M (1970) Ecology of tetranychid mites and
481 their natural enemies: A review. I. Tetranychid enemies: their biological
482 characters and the impact of spray particles. Hilgardia 40:331-390
483 Mori K, Saito Y, Sakagami T (1999) Effects of nest web and female attendance on

484 survival of young in the subsocial spider mite *Schizotetranychus longus* (Acari:
485 Tetranychidae). Exp Appl Acarol 23:411-418
486 Morishita M (1992) Movement of two species of tetranychid mites (Acarina:
487 Tetranychidae) from border vegetation to watermelon fields. Jpn J Appl Entomol
488 Zool 36:25-30 (in Japanese, with English summary)
489 Morishita M (1997) Intercrop movement of the two-spotted spider mite, *Tetranychus*
490 *urticae* Koch (Acari: Tetranychidae) from chrysanthemum to pea field. Jpn J
491 Appl Entomol Zool 41:33-38 (in Japanese, with English summary)
492 Ohno S, Miyagi A, Ganaha-Kikumura T, Gotoh T, Kijima K, Ooishi T, Moromizato
493 C, Haraguchi D, Yonamine K, Uezato T (2010) Non-crop host plants of
494 *Tetranychus* spider mites (Acari: Tetranychidae) in the field in Okinawa, Japan:
495 determination of possible sources of pest species and inference on the cause of
496 peculiar mite fauna on crops. Appl Entomol Zool 45:465-475
497 Oku K, Yano S, Osakabe Mh, Takafuji A (2003) Spider mites assess predation risk
498 by using the odor of injured conspecifics. J Chem Ecol 29:2609-2613
499 Oku K, Yano S, Osakabe Mh, Takafuji A (2005) Mating strategies of *Tetranychus*

500 *kanzawai* (Acari: Tetranychidae) in relation to mating status of females. Ann
501 Entomol Soc Am 98:625-628
502 Oku K, Magalhaes S, Dicke M (2009) The presence of webbing affects the
503 oviposition rate of two-spotted spider mites, *Tetranychus urticae* (Acari:
504 Tetranychidae). Exp Appl Acarol 49:167-172
505 Osakabe Mh (1988) Relationships between food substances and developmental
506 success in *Amblyseius sojaensis* Ehara (Acarina: Phytoseiidae). Appl Entomol
507 Zool 23:45-51
508 Osakabe Mh, Inoue K, Ashihara W (1986) Feeding, reproduction and development
509 of *Amblyseius sojaensis* Ehara (Acarina: Phytoseiidae) on two species of spider
510 mites and on tea pollen. Appl Entomol Zool 21:322-327
511 Osakabe Mh, Hirose T, Sato M (2002) Discrimination of four Japanese *Tetranychus*
512 species (Acari: Tetranychidae) using PCR-RFLP of the inter-transcribed spacer
513 region of nuclear ribosomal DNA. Appl Entomol Zool 37:399-407
514 Ozawa A, Takafuji A (1987) Inter-specific crosses between *Tetranychus urticae*
515 Koch and *Tetranychus kanzawai* Kishida. Jpn J Appl Entomol Zool 31:51-54 (in

516 Japanese, with English summary)

517 Ozawa M, Yano S (2009) Pearl bodies of *Cayratia japonica* (Thunb.) Gagnep.

518 (Vitaceae) as alternative food for a predatory mite *Euseius sojaensis* (Ehara)

519 (Acari: Phytoseiidae) Ecol Res 24:257-262

520 Pallini A, Janssen A, Sabelis MW (1999) Spider mites avoid plants with predators.

521 Exp Appl Acarol 23:803-815

522 Pratt PD, Croft BA (1999) Expanded distribution of the bamboo spider mite,

523 *Schizotetranychus longus* (Acari: Tetranychidae), and predation by *Neoseiulus*

524 *fallacies* (Acari: Phytoseiidae). Acarologia 40:191-197

525 Prokopy RJ, Roitberg BD (2001) Joining and avoiding behavior in non-social insects.

526 Annu Rev Entomonl 46:631-665

527 Rasa OA (1997) Aggregation in a desert tenebrionid beetle: a cost/benefit analysis.

528 Ethology 103:466-487

529 Roda A, Nyrop J, English-Loeb G, Dicke M (2001) Leaf pubescence and two-spotted

530 spider mite webbing influence phytoseiid behavior and population density.

531 Oecologia 129:551-560

532 Sabelis MW, Bakker FM (1992) How predatory mites cope with the web of their
533 tetranychid prey: a fubctional view on dorsal chaetotaxy in the Phytoseiidae.
534 Exp Appl Acarol 16:203-225
535 Saito Y (1983) The concept of “life types” in Tetranychidae. An attempt to classify
536 the spinning behaviour of Tetranichidae. Acarologia 24:377-391
537 Saito Y (1986a) Biparental defence in a spider mite (Acari: Tetranychidae) infesting
538 *Sasa bamboo*. Behav Ecol Sociobiol 18:377-386
539 Saito Y (1986b) Prey kills predator: counter-attack success of a spider mite against
540 its specific phytoseiid predator. Exp Appl Acarol 2:47-62
541 SAS Institute Inc (1998) SAS/STAT user’s guide, release 6.03 edition. SAS Institute,
542 Cary
543 Semeniuk CAD, Dill LM (2004) Cost/benefit analysis of group and solitary resting
544 in the cowtail stingray, *Pastinachus sephen*. Behav Ecol 16:417-426
545 Shirotsuka K, Yano S (2011) How to avoid cannibalism within laboratory predatory
546 mite populations under successive rearing. Jap J Appl Entomol Zool 55:25-27
547 (in Japanese with English legends)

548 Spieler M (2003) Risk of predation affects aggregation size: a study with tadpoles of
549 *Phrynomantis microps* (Anura: Microhylidae). Anim Behav 65:179-184
550 Strong WB, Croft BA, Slone DH (1997) Spatial aggregation and refugia of the mites
551 *Tetranychus urticae* and *Neoseiulus fallacis* (Acari: Tetranychidae,
552 Phytoseiidae) on hop. Environ Entomol 26:859-865
553 Takafuji A, Morishita M (2001) Overwintering ecology of two species of spider
554 mites (Acari: Tetranychidae) on different host plants. Appl Entomol Zool
555 36:169-175
556 Tilman D (1982) Resource Competition and Community Structure. Princeton
557 University Press, Princeton
558 Vasconcelos HL (1991) Mutualism between *Maieta guianensis* Aubl., a
559 myrmecophytic melastome, and one of its ant inhabitants: ant protection
560 against insect herbivores. Oecologia 87:295-298
561 Yano S (2008) Collective and solitary behaviors of the two-spotted spider mite
562 (Acari: Tetranychidae) are induced by trail following. Ann Entomol Soc Am
563 101:247-252

564 Yano S, Wakabayashi M, Takabayashi J, Takafuji A (1998) Factors determining the
565 host plant range of the phytophagous mite, *Tetranychus urticae* Koch (Acari:
566 Tetranychidae). A method for quantifying host plant acceptance. Exp Appl
567 Acarol 22:595-602
568 Yano S, Kanaya M, Takafuji A (2003) Genetic basis of color variation in leaf scars
569 induced by the Kanzawa spider mite. Entomol Exp Appl 106:37-44
570

571 **Figure Legends**

572 **Fig. 1** A preliminary test confirming predation saturation over time. There was no
573 predation of spider mite females after the initial 12 h. Hence, predation rate was
574 measured subsequently 24 h after predator introduction.

575

576 **Fig. 2** Effects of group size and webs on predation rates on spider mites. *Bars*
577 indicate per capita predation rate on active (a) *T. urticae* and (b) *T. kanzawai* with
578 different group sizes and time lags for web building. Decreased predation with
579 increased time lag indicates that completed webs may effectively defend spider mites
580 from predation while decreased (per capita) predation with increasing group size
581 indicates a dilution effect.

582

583 **Fig. 3** Degree of spider mite group living in response to a predator. Distances
584 between conspecific spider mites are shown in relation to predator presence 1, 4, and
585 24 h after predator introduction. Spider mites lived more closely together in response
586 to predator presence, although the differences became less obvious over time after

587 predator introduction.

588

589 **Fig. 4** Indirect interactions between spider mites sharing a web in the absence of a

590 predator. The number of eggs laid by a test female within 24 h did not differ among

591 treatments for either a *T. urticae* and b *T. kanzawai*, indicating that there was

592 virtually no indirect interaction between heterospecific and conspecific mites sharing

593 fresh webs.

594

595 **Fig. 5** Do spider mites living together distinguish between species? *Lines* indicate

596 distances between spider mite females. There were no significant differences among

597 the three groups at any point, suggesting that spider mite females living together do

598 not distinguish between species.

Fig.1

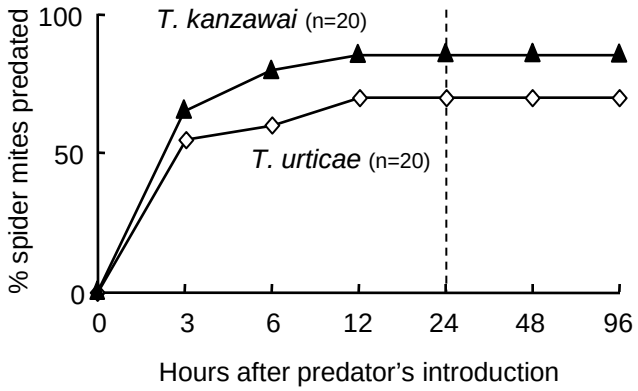

100
50
0
% spider mites predated
T. kanzawai (n=20)
T. urticae (n=20)
0
3
6
12
24
48
96
Hours after predator's introduction

Fig.2

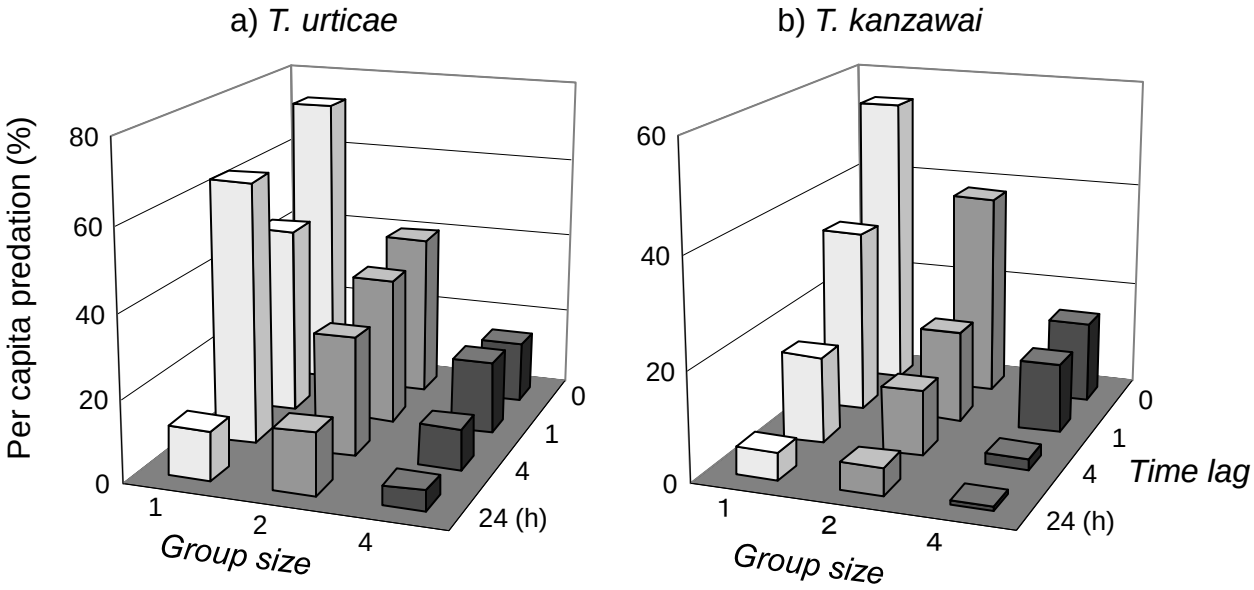

a) T. urticae
b) T. kanzawai
Per capita predation (%)
80
60
40
20
0
1
2
4
Group size
0
1
4
24 (h)
Time lag

Fig.3

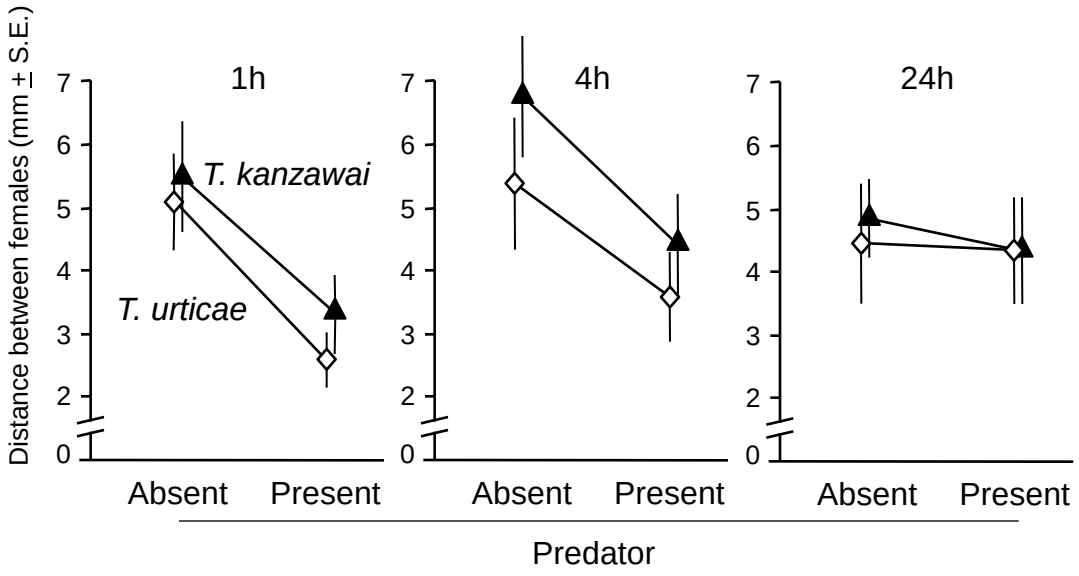

Distance between females (mm ± S.E.)
1h
4h
24h
T. kanzawai
T. urticae
0
2
3
4
5
6
7
Absent
Present
Predator

Fig.4

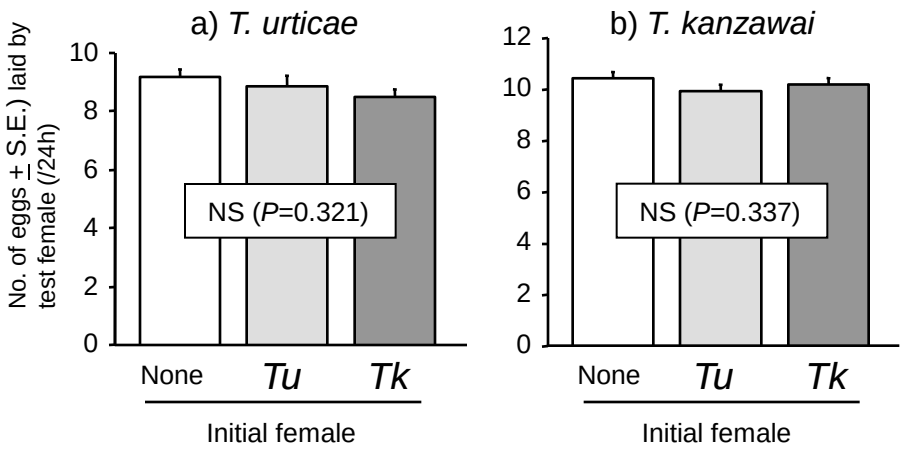
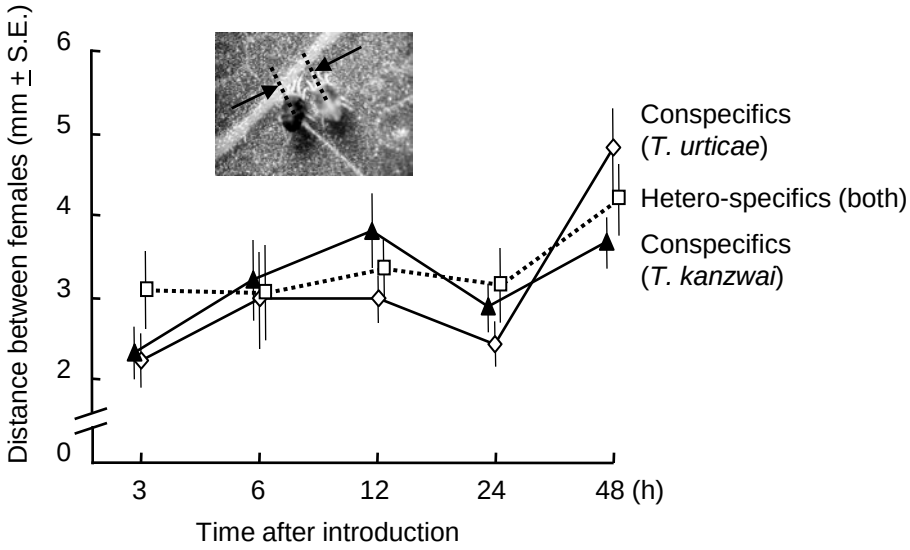

a) T. urticae
b) T. kanzawai
No. of eggs + S.E.) laid by test female (/24h)
10
8
6
4
2
0
12
NS (P=0.321)
NS (P=0.337)
None
Tu
Tk
Initial female

Fig.5


Distance between females (mm ± S.E.)
6
5
4
3
2
0
3
6
12
24
48 (h)
Time after introduction
Conspecifics
(T. urticae)
Hetero-specifics (both)
Conspecifics
(T. kanzwai)